

Emergent computation in simple model of neural activity

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We investigate the dynamics of a network consisting of an array of identical cortical units with nearest neighbor interactions under periodic arousal. Each unit consists of two interconnected populations of neurons tuned to a state in which many nonlinear resonances are available. The network is critically balanced due to short-ranged antisymmetric connections between units. For wide ranges of the network parameters, the patterns of activity resemble the dynamics of cellular automata. It is argued that these dynamical states may provide a template in which computation can be implemented.

I. INTRODUCTION

Understanding the mechanisms by which information is processed in the nervous system is one of the major challenges in neuroscience. Neural oscillations underlie a wide range of functions like locomotion and maintenance processes such as breathing (see Buzsáki et al. for a review¹). There is a growing view that rhythmic neural activity also plays an active role in shaping neural processing and behavior by transiently binding cells into synchronized assemblies². This has lead many authors to the conjecture that neural oscillations support an even larger variety of neural functions, including cognition³. However, a quantitative description of the processes by which higher level functions - such as consciousness - emerge out of the aggregate activity of millions of neurons remains one of nature's best kept secrets.

In this work we explore the hypothesis that nonlinear resonances underlie the generation of complex rhythms in brain activity. For this I propose a simple model consisting of identical cortical columns which interact laterally with their nearest neighbors and receive periodic arousal from an external structure. The local dynamics of the columns is tuned to a state in which many nonlinear resonances may occur in response to the periodic arousal. In the absence of lateral interactions, the dynamics of each column consist of a periodically forced two-dimensional neural oscillator in which several dynamical bifurcations are available. Upon small modulations of the periodic arousal, the oscillators can display period doubling bifurcations and other signatures of low dimensional chaos^{4,5}. Because of the low dimensionality, the dynamics of the constituent units in the model can be characterized by sets of integers using topological

methods^{6,7}. When the units interact, the dynamics of the network presents complex spatio-temporal patterns of activity which in some cases resemble the type of behavior exhibited by class III and IV cellular automata⁸. The main finding of this article is that a simple layer of identical cortical units under certain conditions, can not only display a multitude of complex oscillations but can also implement clockwork dynamics which may provide a basis for computation⁹.

II. THE MODEL

The central assumption in the model is that the cortical units are tuned to a state in which many nonlinear resonances are within the range of the periodic arousal, ie: each column can be entrained subharmonically to an incoming signal¹⁰. A procedure to tune neural circuits towards these regimes can be found in¹¹. The second assumption is that the system is critically balanced. The notion that biological systems operate at a critical point has been explored by several authors¹²⁻¹⁴. Operating at this special point prevents the network from saturating by balancing excitation and inhibition. Importantly, in order for information to propagate efficiently throughout the network, inhibition and excitation have to be balanced locally¹⁵. This is achieved by assuming antisymmetric interactions between columns; each column inhibits/excites its two neighbors and are placed in a checkerboard configuration as shown in figure 1. The model consist of N identical cortical columns, each composed of 2 interacting subpopulations of neurons (x_L, y_L) which form a local circuit. The dynamics of each subpopulation is given by the celebrated Wilson Cowan model^{16,17}. The columns interact laterally only with their nearest neighbors and they all receive periodic forcing from an external structure which represents generalized CNS arousal^{18,19}. The state of the system can be specified by a $2N$ dimensional vector x where each component corresponds to the activity of a subpop-

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ulation. The model can be expressed in a compact way,

$$\dot{x} = -x + S(Cx + \rho + \gamma(t)). \quad (1)$$

Here C is the connectivity matrix, ρ is a constant input or bias, $S(x) = \frac{1}{1+e^{-x}}$ is the sigmoid function, and γ is a periodic signal which represents thalamic input. Matrix C defines the architecture of the model and can be expressed as the sum of two matrices,

$$C = L + kW. \quad (2)$$

Matrix L is a $2N \times 2N$ block diagonal matrix where each block L_C corresponds to the local connectivities of the subpopulations within a column. The dynamics of the columns in the absence of lateral interactions is governed by this matrix and the bias term ρ which represents a constant input to each subpopulation. The interaction between columns is defined by matrix W . Because each column consists of 2 subpopulations, it is convenient to regard W as a $N \times N$ matrix whose elements are 2×2 blocks w that define the interaction between adjacent sites. The strength of the coupling is controlled by parameter k . In this work we assume that all columns and interactions between columns are identical. We also assume that the columns interact only via the first subpopulation. The important assumption that excitation and inhibition are balanced in local patches is achieved by imposing anti-symmetric interactions between columns $W_{ij} = -W_{ji}$. For simplicity, we consider nearest neighbor interactions. This yields a matrix W with blocks w of alternating sign in both the upper and lower diagonals. Let $L_c = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$

and $w = \begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix}$ be the local connectivities within a column and the interaction matrix between columns respectively. Then C is a $N \times N$ matrix whose elements are 2×2 blocks,

$$C = \begin{bmatrix} L_c & -kw & 0 & \dots & 0 \\ kw & L_c & kw & \ddots & \vdots \\ 0 & -kw & \ddots & \ddots & 0 \\ \vdots & \ddots & \ddots & L_c & -kw \\ 0 & \dots & 0 & kw & L_c \end{bmatrix}. \quad (3)$$

We assume periodic boundary conditions by setting $C_{1,N} = -kw$ ($C_{N,1} = kw$). The constant input ρ is the same for all columns. This is a $2N$ dimensional vector with N copies of parameters

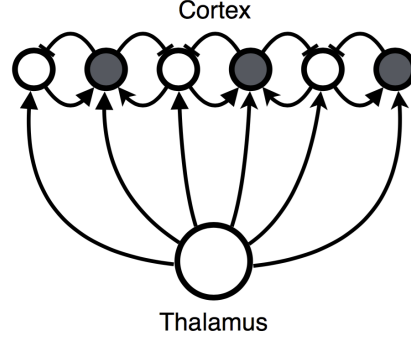


FIG. 1. Toy model of cortex and thalamus. A uni-dimensional array of cortical columns with nearest neighbor interactions. All columns are identical and receive the same periodic arousal from the thalamus. Each column consists of two interconnected populations of neurons tuned to be close to nonlinear resonances. The arrows indicate excitatory connections and the Ts correspond to inhibitory ones. The network is critically balanced: the columns inhibit or excite their nearest neighbors and are placed in an alternating checkerboard configuration.

$\rho_i = [\rho_x, \rho_y]$ where ρ_x and ρ_y are the constant inputs to each subpopulation within a column. In addition to the lateral interaction and their intrinsic dynamics, all the columns receive periodic arousal from an external structure. We assume a particular family of periodic signals γ defined by

$$\gamma(t) = AS(\eta(\cos(\omega t) - \mu)). \quad (4)$$

Here A is the amplitude and ω is the frequency of the oscillation. The parameters $\eta = 0.75$ and $\mu = -1$ are used to control the waveform of the arousal signal and are kept fixed. We assume that all columns receive the same input in the first subpopulation only. This is achieved by promoting A to a vector of dimension $2N$ with N identical copies $\{A, 0\}_i$. The model is specified by a total of 12 parameters: the local connectivities ($a = 4.92, b = -6.76, c = 14.96, d = 18.76$) and the constant inputs or bias to each column ($\rho_x = -3.00, \rho_y = -14.96$), the lateral coupling strength k , the amplitude A and frequency $\omega = 1$ of the periodic signal, the waveform parameters ($\eta = -1, \mu = 0.75$) and the number of columns N . A more detailed discussion on how to tune the columns can be found in¹¹. In this work, all parameters were kept fixed except the lateral coupling k and the periodic arousal amplitude A .

III. RESULTS

The rest of the article consists of numerical explorations of the model. Figure 2 shows the dynamics of the network for increasing values of the lateral coupling k . The arousal amplitude is kept fixed at $A = 2.5$. The network consists of $N = 500$ columns and was evolved from random initial conditions for 10^6 time steps using a Runge-Kutta O(4) routine with $dt = 0.01$. As k is increased the network activity displays a multitude of spatio-temporal patterns, some of bewildering complexity. For $k = 0.55$ (2A) the network displays patches of local synchrony on a disordered background. For $k = 1.55$ (2B) the emergence of structures becomes more apparent. When observed over long periods of time, the network activity very much resembles the kind of patterns which emerge from 1D cellular automata⁸. Cellular automata are discrete dynamical systems consisting of a grid of cells that can take any of a finite number of states, and an update rule which maps the neighborhood of a cell into a new state. Even in the simplest cases of two-state cells with nearest neighbors rules, the behavior of these systems is extremely complex. Extensive quantitative studies on 1D automata have led to a classification scheme into 4 universal classes²¹. Automata in class I and class II quickly evolve into homogeneous states and stable or oscillating structures. Class III automata evolve in a chaotic manner and Class IV automata evolve into complex structures that interact in conspicuous ways²⁰. The network activity seems to exhibit this class of behavior for $k = 0.902$ in Fig. (2C). The system displays a set of structures traveling sideways with finite speed and mutual interactions. These structures in turn seem to be carrying information. A more ordered pattern occurs for $k = 1.111$ (Fig. (2D)). This solution is discussed in more detail later in this section. Finally, the solutions in Figs. (2E) and (2F) ($k = 1.5$ and $k = 2.777$) exhibit remarkable complexity and appear to be consistent with either class III or IV.

A closer inspection of the model solutions is shown in Figure 3. In this case, there seem to be structures with irregular shapes on a uniform background. The substrate of these structures is revealed by the time series of a representative neuron in Fig. 3B ($x = 391$). They consist of disruptions of local synchrony between adjacent columns. Interestingly, these disruptions are sparse in both the spatial and temporal domains. A second neuron ($x = 171$) was chosen because of its switching dynamics. This unit operates in two different dynamical regimes. For a period of time (highlighted in the figure) this column seems to host a persistent structure which later dissolves into the background. Outside this interval, the behavior

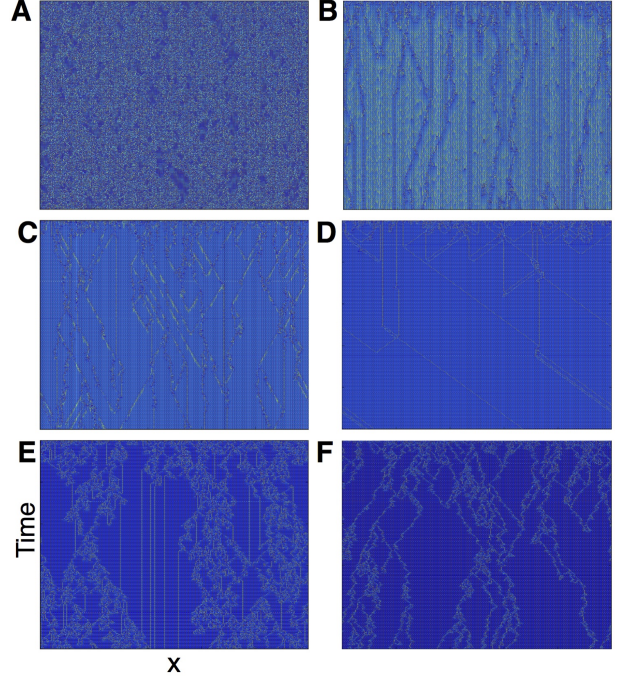


FIG. 2. **Network activity for increasing values of the lateral coupling k .** As the interaction between columns is increased the network presents multiple patterns of complex activity. The system is evolved for 10^6 time steps from random initial conditions. Raw traces are shown. The activity of each column is color coded (0 blue, 1 red). [This figure may not print correctly, see the electronic version]

of this column does not seem to differ from the rest of the units. The same column that retained some spatial information is at a different time serving as a template for propagation of structures. Surprisingly, the units in this system are implementing a multiplicity of tasks without external intervention.

For wide ranges of the parameter values the model exhibits the basic operations of information transmission, storage, and modification, suggesting the capacity to support computation⁹. This is illustrated in Figure 4. The network activity for $k = 1.111$ (Fig. 2D) was averaged over a period of time of $\approx 5\tau$ to highlight departures from baseline activity. The shaded region contains several features which can be related to information processing. For clarity, only the time traces for the excitatory neurons are shown. Information is encoded in spatial inhomogeneities of the dynamics. While most of the neurons are at any given instant synchronized with their closest neighbors, local disruptions of spatial synchrony seem to persist for arbitrarily long periods of time. These disruptions can be both stationary in space and travel to distant places. In Figure 4, there are persistent structures which are stationary in space

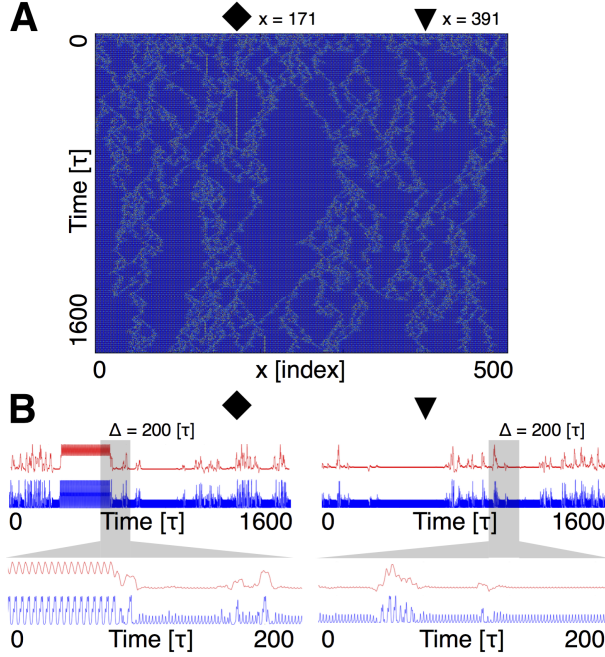


FIG. 3. **Computation implemented on oscillatory background.** (A) The intricate patterns consist of traveling disturbances - local disruptions of synchrony - on an oscillatory background. The network presents long lived structures which propagate and interact with each other on timescales that are several order of magnitude slower than the periodic arousal. Time is indicated in units of the arousal period $\tau = \frac{2\pi}{dt} \approx 630$ integration steps (B) The time series for two neurons are shown. The top rows correspond to the full integration range and the bottom rows show a blow up of the activity in shorter intervals indicated by the shades. The red (top) curves correspond to a time average of the activity over $\approx 5\tau$ to help visualization and the blue (bottom) curves are the raw traces. [This figure may not print correctly, see the electronic version]

and look like straight colored lines. They consist of a larger wave enclosed by two smaller waves which barely differ from the background. In most cases it appears that this type of structure requires external interaction to change. However, in the highlighted region, two of these structures seem to carry additional information. In one case (Fig. 4C), for no apparent reason, the whole structure makes a sudden move to the left. One may speculate that this structure is carrying information on where to go. If such be the case, it may suggest a mechanism for the routing of information in the brain. The second structure follows suit and at some point in its evolution begins moving right as it dismembers into two smaller traveling structures (Fig. 4A). Figure 4D shows modification of the structure in Fig. 4C. As an incoming beam of smaller traveling structures

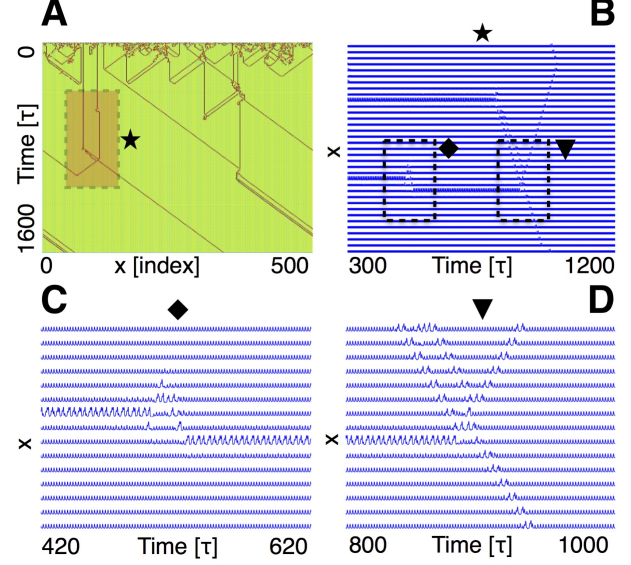


FIG. 4. **Emergent cellular automata dynamics.** The dynamics of the network implements clockwork computations. (A) Time average of the network activity on Fig. (2D). The region of interest is indicated by the shade. (B) Raw traces of excitatory neurons for the region indicated in (A). (C) A self-routed message? A structure involving three neurons exhibits a self sustained spatial inhomogeneity consisting of a larger wave enclosed by smaller waves (which differ from the background). The whole structure makes a sudden move to a neighboring set of columns. (D) The structure interacts with an incoming signal and dismantles into shorter temporal structures which travel in space without deformations.

collides with the not-so-stationary larger structure, the former dismembers into two smaller and identical bleeps of asynchrony which travel in opposite directions with equal speed. Notably, the waveform associated with a bit of information travels without deformation while embedded in an otherwise regular background of oscillatory activity.

A traditional approach to the study of cellular automata consists of regarding the initial condition as an input, while the evolution of the system is considered to be the output of a computation performed on that initial state²⁰. Following this paradigm the evolution of a simple initial condition is investigated in Figure 5. The initial state consists of having all columns set to 0 except one at the center which is set to 1. Different values of the arousal amplitude yield radically different patterns or computations ($A \in [1.5, 4]$ and $k = 1$). In some cases, the system “remembers” the input by producing a predictable pattern (5A, 5B) while in others complex structures emerge. This points out an interesting feature of the model: the processing of any given

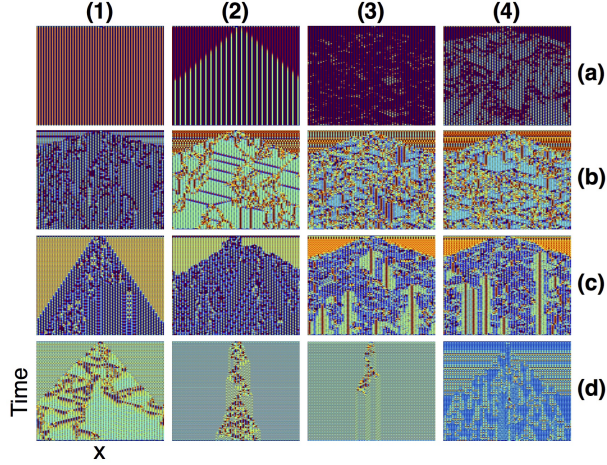


FIG. 5. **Evolution of a point perturbation for different values of stimulation amplitude A .** An initial state consisting of a single neuron active in the center evolves into radically different patterns as the amplitude of the periodic stimuli is changed (increasing in lexicographical order). The network consists of $N = 200$ columns and was evolved for 2×10^5 integrations steps. Time averaged activity is color coded (0.1 blue, 0.3 red).

state depends on the arousal function or stimuli¹⁸. In this model the same substrate can be utilized to implement diverse tasks either by direct modulation of the thalamic activity or by closing the loop by feeding a measure of cortical activity back into the thalamus. Finally, Figure 6 shows the long term behavior of the same network ($A = 2.55$ and $k = 1$) for several random initial states. In most instances (left) the network activity quickly dissolves into the background. However, approximately 5% of the initial states trigger transient dynamics which take much longer to decay (right). This behavior is consistent with that of class IV cellular automata and therefore suggests that the simple model presented here may have the capacity to support computation²¹.

IV. CONCLUSIONS

The purpose of this article is to present a simple model of neural dynamics which displays complex emergent features. Despite the simplicity of the system, its solutions exhibit a multitude of spatio-temporal patterns which resemble the dynamics of discrete 1D cellular automata. This provides a potentially important link among complexity theory, nonlinear dynamics and neuroscience.

Cellular automata have been regarded as models of complexity and their computational properties have been extensively characterized⁸. Previous studies suggest that these systems may support the

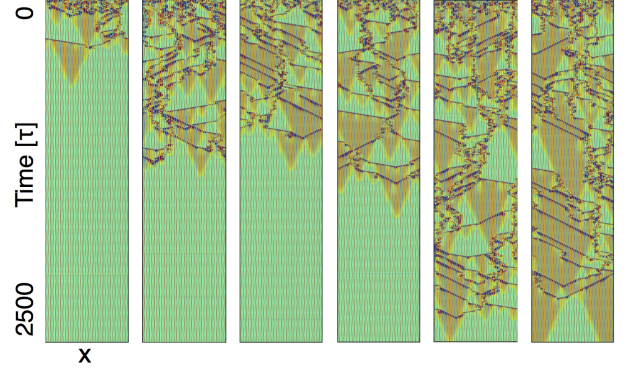


FIG. 6. **Long term behavior of random initial states.** Transient activity persists for long periods of time. The network ($N = 200$) was evolved for 1.6×10^6 integrations steps ($\approx 2500\tau$) with $A = 2.55$ and $k = 1$. Time averaged activity is color coded (0.05 blue, 0.3 red).

essential features required for information processing and that these qualities are enhanced near points in parameter space in which transitions to chaotic behavior occur⁹. Even though the numerical exploration of these systems is very efficient due to their discrete nature, this also makes it hard to conceive concrete applications since in many cases physical systems are considered to be continuous. The fact that clockwork dynamics occurs in a continuous system leads to the intriguing conjecture that there may be a correspondence between the model parameters and a rule for an automaton which would replicate the continuous solutions when observed stroboscopically. This would provide an elegant description of what is an otherwise intractable, out of equilibrium, many-body nonlinear problem. Further investigation on the mathematical aspects of this model may yield fruitful insight towards a quantitative theory of biological phenomena^{22,23}.

Future directions should include the computationally more intensive exploration of 2D and 3D extensions of the model. Cellular automata in two dimensions can display beautiful dynamics which resemble some aspects of living systems. Conway's “*Game of Life*” (GOL) is perhaps the best known example of this class²⁴ and has tantalized researchers in artificial intelligence for decades. The results presented in this article suggest that as the parameters of the model are swept, the emerging automaton-like dynamics exhibits the four classes of universality proposed by Wolfram, including most significantly classes III and IV⁸. This suggests that dynamical patterns with properties similar to that of GOL may occur in this system for higher dimensions. A link between this type of behavior and neural dynamics could potentially provide a basis for describing

higher-order neural functions such as cognition.

An extension of the model can be built by feeding back cortical activity into the thalamus. This would provide simple models with yet another fold of complexity in their solutions. A readout function which integrates cortical activity for a certain amount of time, or highlights specific features in the patterns, could then be used to modify the weights and phases of the cortico-thalamic connections, or the dynamics of the thalamic input itself. This would lead to a model in which a computation takes place and then self-modifies its rules according to the output of the previous process. Simple models of the sort presented here can be used as building blocks for larger and more biophysically accurate models of cortical dynamics. Finally, while the model is presented in the context of neuroscience, the mechanisms at play may be applicable to a wider array of systems. The assumptions of the model are that the units can be entrained sub-harmonically to a master oscillator and that the network is critically balanced. Many biological systems can be modeled as nonlinear oscillators with short-range interactions²⁵. Also, there is growing evidence that biological networks operate near a critical regime¹². Therefore, models of the sort presented here could provide a basis to describe a variety of biological phenomena. The fact that a simple array of coupled nonlinear oscillators displays complex behavior makes it unlikely that evolution would have missed this opportunity.

V. ACKNOWLEDGMENTS

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